

Zeitschrift: Bulletin de la Société Neuchâteloise des Sciences Naturelles
Herausgeber: Société Neuchâteloise des Sciences Naturelles
Band: 120 (1997)

Artikel: The genus Pandanus (Pandanaceae) in Madagascar (Part 1)
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DOI: <https://doi.org/10.5169/seals-89456>

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THE GENUS *PANDANUS* (PANDANACEAE) IN MADAGASCAR (PART 1)

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Mots-clés: Afrique, Madagascar, *Pandanus* sect. *Martellidendron*, Pandanacées, Bisexualité potentielle, Staminodes, Taxonomie

Key-Words: Africa, Madagascar, *Pandanus* sect. *Martellidendron*, Pandanaceae, potential Bisexuality, Staminodes, Taxonomy

Résumé

Une espèce nouvelle de *Pandanus* sect. *Martellidendron* de Madagascar est décrite (*P. nosibicus* Huynh). Sa drupe est pourvue de staminodes à la base, révélant ainsi pour la première fois que la fleur femelle de cette section est potentiellement bisexuelle par le fait d'avoir aussi l'autre sexe à l'état non fonctionnel, comme l'est sa fleur mâle. Ces staminodes ont quatre sacs polliniques sans pollen: c'est la première fois dans le genre *Pandanus* que des staminodes à quatre sacs polliniques (comme les étamines) ont été observés; la présence de ces staminodes est une autre nouvelle caractéristique de cette section. Etant donné qu'une bisexualité potentielle dans la fleur femelle et dans la fleur mâle, et des staminodes à quatre sacs polliniques, ont été observés aussi dans le genre *Freycinetia*, un autre genre de la famille des Pandanacées, la possession de ces deux caractères par cette section renforce la relation étroite entre elle et ce genre, révélée auparavant par leur possession commune d'une exine à trois couches, et contribue ainsi à indiquer que cette section constitue probablement le lien phylogénétique entre ces deux genres. Une autre nouvelle caractéristique de cette section est trouvée: ses drupes à l'état mûr ne sont pas connées dans le syncarpe. La feuille de *P. hermaphroditus*, une autre espèce de cette section, est décrite pour la première fois, en utilisant son type.

Summary

A new species of *Pandanus* sect. *Martellidendron* from Madagascar is described (*P. nosibicus* Huynh). Its drupe has staminodes around its base, thus revealing for the first time that the pistillate flower of the section is potentially bisexual in also having the other sex in unfunctional condition, as is its staminate flower. The staminodes have four pollensacs without pollen: this is the first time in the genus *Pandanus* that staminodes with four pollensacs like stamens were observed; the presence of these staminodes is another new characteristic of the section. Since potential bisexuality in both pistillate and staminate flowers, and staminodes with four pollensacs, were both also observed in *Freycinetia*, another genus of the family Pandanaceae, the possession of these two fea-

tures by this section reinforces a close relationship existing between them revealed earlier by their common possession of a 3-layered exine, and contributes therefore to indicate that most probably, this section constitutes the phylogenetic link between the two genera. Another new characteristic of the section is found: its drupes at maturity are unconnate in syncarp. The leaf of *P. hermaphroditus*, another species of the section, is described for the first time, using its type.

Zusammenfassung

Eine neue Art *Pandanus* sect. *Martellidendron* aus Madagaskar (*P. nosibicus* Huynh) wird beschrieben. Ihre Drupa besitzt an der Basis Staminodien, was zum ersten Mal zeigt, dass die weibliche Blüte dieser Sektion potentiell bisexual ist, da sie das andere Geschlecht im nicht funktionellen Zustand auch besitzt, gleich wie die männliche Blüte. Diese Staminodien haben vier Pollensäcke ohne Pollen: zum ersten Mal werden bei der Gattung *Pandanus* Staminodien mit vier Pollensäcken wie bei den Staubblättern beobachtet; das Vorhandensein solcher Staminodien ist ein weiteres neues Merkmal dieser Sektion. Eine potentielle Bisexualität bei der weiblichen und männlichen Blüte sowie Staminodien mit vier Pollensäcken wurden auch bei der Gattung *Freycinetia*, einer anderen Gattung der Familie Pandanaceae, beobachtet. Das Vorhandensein dieser beiden Merkmale bei dieser Sektion verstärkt die enge Verwandtschaft zwischen ihr und der Gattung *Freycinetia* (die bereits früher durch das Vorhandensein einer 3-schichtigen Exine bei beiden gezeigt wurde) und trägt dazu bei, dass diese Sektion wahrscheinlich die phylogenetische Verbindung zwischen diesen zwei Gattungen ist. Ein anderes neues Merkmal dieser Sektion wird gefunden: die Drupen im Reifestadium sind im Synkarp nicht konnat. Das Blatt von *P. hermaphroditus*, einer anderen Art dieser Sektion, wird zum ersten Mal auf der Basis ihres Typs beschrieben.

INTRODUCTION

Pandanus is widespread on Madagascar, which appears as one of the three great centres of differentiation of both species and sections in this genus. In particular, all or almost all of the species found in the island are endemic, and several sections such as *Martellidendron*, *Acanthostyla*, *Stephanostigma*, are not observed elsewhere.

Several authors studied the taxonomy of *Pandanus* in Madagascar, the most prominent appeared to be MARTELLI & PICHISERMOLLI (1951), ST. JOHN (1968), and STONE (1970a, 1970b, 1975). A review of the genus in the island was made by STONE (1970b), who also elaborated keys for the sections. Later Stone continued his study at intervals until his passing on 19 March 1994.

Thus, a very large number of taxonomically utilizable specimens collected from the seventies have not been investigated, especially in the Herbarium of the Muséum National d'Histoire Naturelle, Paris, and in that of the Missouri Botanical Garden, St. Louis. Recently, Michel Omer Laivao, of Madagascar, has undertaken a doctorate thesis on the *Pandanus* in Madagascar at the Laboratoire de Phanérogamie, University of Neuchâtel. Several other specimens were therefore collected by him, also for the Herbarium of Neuchâtel. Others were collected by Martin Callmänder (Laboratoire de Phanérogamie, University of Neuchâtel) and Laivao in September 1996. A preliminary investigation of these specimens by the present author revealed the existence of several unknown species to be

described. This was to be expected firstly since a large number of these specimens was collected in regions where the genus has not been studied or only superficially, and secondly given the widely variable morphology of the genus in Madagascar. Other unknown species will certainly be found, especially as the Missouri Botanical Garden and Laivao will continue and extend their collections.

The present paper describes one of the new species which were identified.

OBSERVATIONS

Pandanus nosibicus Huynh, sp. nov. (sect. *Martellidendron*)

Arbor 4-6 m alta; trunco 15 cm diametenti, radicibus gralliformibus suffulto. Folia circa 250 cm longa 6 cm lata in medio 7 cm in 1/6 infera, subcoriacea flexibilia in 1/6 supera, coriacea rigida in reliqua, e basi laminae ad basim caudae 7-8 cm longae perspicue biplicata-canaliculata, in sicco viridula vel viridi-brunnea pariter in ambabus paginis, tessellata in pagina adaxiali non tessellata in abaxiali; marginibus (in lamina applanata) sub angulo circa 6° infra caudam convergentibus; plicis inermibus; canale medio usque ad apicem caudae visibili; denticulis atro-brunneis in apice, stramineis in reliqua; denticulis marginalibus e basi laminae ad apicem praesentibus, prope basim ad 3.5 mm longis interdum perpendicularibus vel subperpendicularibus, sursum versus brevioribus antrorsis; denticulis costalibus in 2/3 superis tantum praesentibus, semper antrorsis, generaliter brevioribus densioribusque quam marginalibus sub isdem libramentis. Syncarpium solitarium, circa 25 cm longum 15 cm latum, oblongo cylindraceum, apice basique leviter rotundatum, pedunculo 38-40 cm longo cum 12-17 bracteis suffultum. Drupae clavatae, 3.9-4 cm longae 1.7-1.9 cm latae 1.2-1.8 cm crassae, ex apice ad basim nitentes

(igitur epicarpio tote integro: drupae in syncarpio non connatae) praecipue infra pileum, 4-5 mm in nucleo syncarpium locatae et non nitentes, 5-6-angulatae (angulis visibilibus sed non prominentibus), basi staminodiis circumdatae; pileo subdistincto, 3-4 mm alto, plano in aspectu laterali valleculato in apicali; stigmatibus semper 2 et spisse oppositis, 2.5-3 mm longis latis, basi peripheriaque connatis, 1 mm stipitatis; endocarpio circa 2.4 cm alto, 0.3 cm ab apice drupae distant 1.3 cm a basi, superne subplano non-cuspidato 4-5 mm crasso, lateraliter hic illic inciso 2.5-2.9 mm crasso; mesocarpio supero 2-2.5 mm alto, medullosa, fibroso; mesocarpio infero 1.3 cm alto, peripheria fibroso, medio medullosa; semine effecto uno, circa 1.6 cm longo 0.6 cm lato, albido, centro circiter 4/10 superis locato. Staminodia filamenta antheraque composita; filamenta laevi, lignosa (epidermide inclusa), sectione transversali oblongo elliptica; anthera rotundata acuminata, 4 loculis separatis praedita (fig. 1-12).

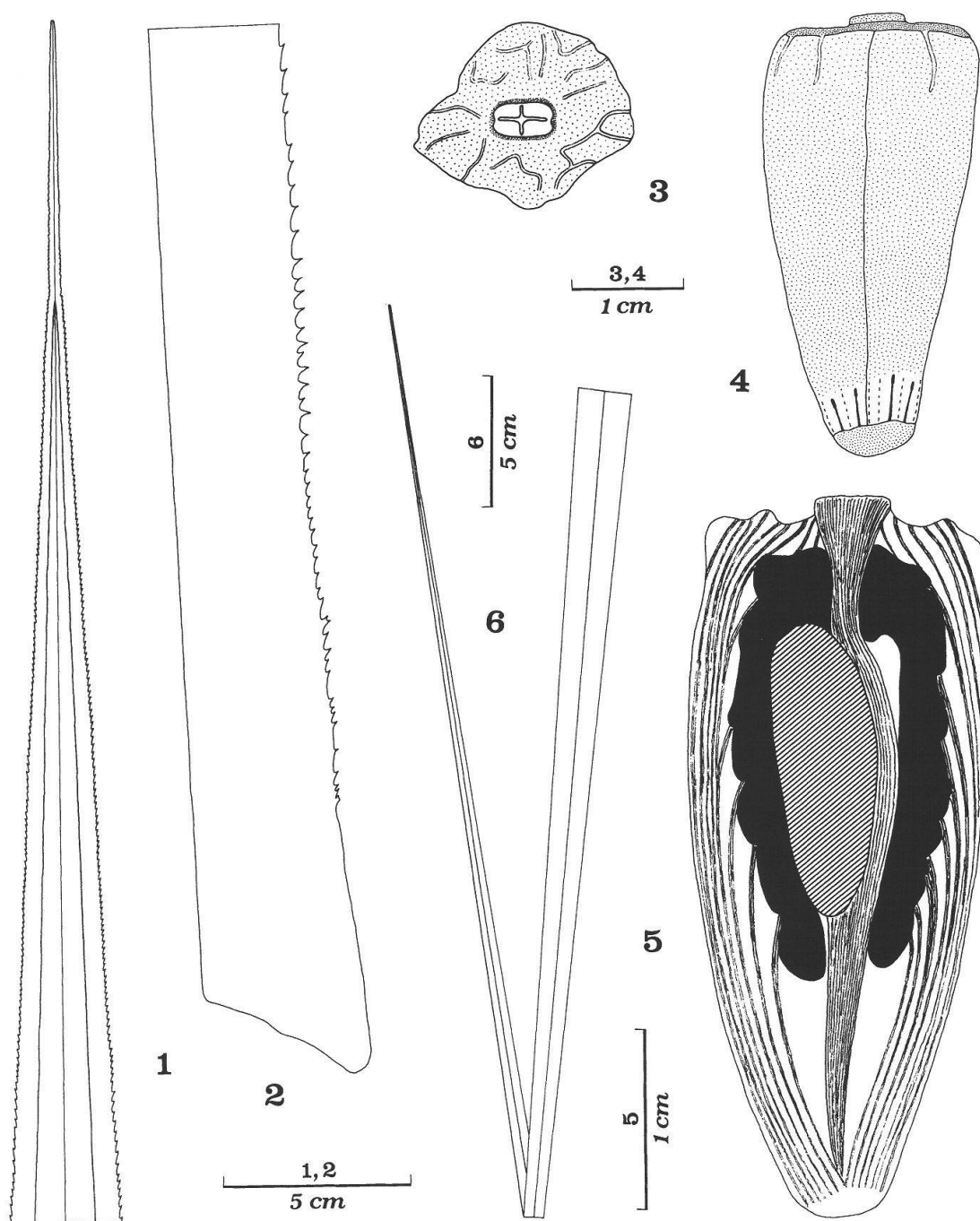
Type: *Laivao NEU 2* (holo- NEU!), Madagascar, Nosy Be, Natural Reserve of Lokobe, Andranonankomba river, on beach, 13°25'13" S 48°19'00" E, 7 May 1996.

The colour photos of infructescences taken in situ by Laivao show the following features. The syncarps were all single and oblong cylindric (fig. 12); the stigmas slightly sunken in the pilei; all the bracts brown and withered; on the maturing syncarps, the stigmas first turned from green to yellowish, then the pilei, resulting in yellowish syncarps with some orange tint on some drupes.

P. nosibicus is named after Nosy Be where it was found.

Identity of Pandanus nosibicus

Pandanus sect. *Martellidendron* to which *P. nosibicus* belongs is an outstanding group. Its drupes are very characte-



Figures 1-6: *Pandanus nosibicus* (holotype) (1-5) & *P. hermaphroditus* (type in P!) (6). 1: Upper part of leaf flattened horizontally, showing adaxial face. 2: Basal part of leaf folded along midnerve (this on left), showing abaxial face. 3: Drupe in apical view. 4: Same drupe in lateral view, showing pileus (densely dotted above), non nitid part (densely dotted below), four staminodes, and longitudinal grooves (interrupted lines) where other staminodes were presumably located. 5: Same drupe in longitudinal section passing by centres of stigmas, showing endocarp (black), seed (hatched), and sterile locule on right of seed. 6: Upper part of leaf (or bract: see text), the apical part showing adaxial face (prickles not represented).

ristic in that they have two close and opposite stigmas whose four arms delimit a cross between them (fig. 3). Apparently no other stigma numbers were found in the section. This invariability in the stigma numbers is a rare feature in the family Pandanaceae. In addition, the endocarp, which envelops the seed locules, does not extend between these (fig. 5). In those other sections of *Pandanus* which have drupes with 2 or more stigmas, by contrast, the endocarp extends between the seed locules (see for example HUYNH 1985: fig. 14 and 15). Its staminate flowers invariably bear a pistillode with two carpel-
 lods (MARTELLI & PICH-SERMOLLI, 1951; HUYNH, 1981): sect. *Martellidendron* is the only section known in the genus to have staminate flowers normally provided with a pistillode. Its anthers also are unique in the family, in that both the lateral parts of the connective and the proximal parts of the anther walls do not have endothelial thickenings (HUYNH, 1983). By contrast, in all the other species of *Pandanus* whose anther structure was studied, the lateral parts of the connective and the proximal parts of the anther walls have endothelial thickenings. Likewise, its pollen grain has a reticulum with small lumina (HUYNH, 1981) and a 3-layered exine (HOTTON *et al.*, 1994): neither character was observed in any other section of *Pandanus*.

Two other characteristics were found in the course of the present study. Firstly, although the drupes of *P. nosibicus* preserved on the type were separated from each other when collected, their epicarp was intact. In fact, the epicarp was nitid from apex to base, thus revealing that at no stage of development are the drupes of this species connate in syncarp. In an unknown species of the section collected in the Masoala Peninsula in September 1996 (*Callmänder & Laivao NEU 8*) and in which the present author was able to observe a whole syncarp, all the drupes were also unconnate. Therefore, the fea-

ture that drupes at maturity are free from each other in syncarp is certainly common to the members of the section. This would suggest that the description of the drupe of *P. cruciatus* as being with «parte inferiore connata» (MARTELLI & PICH-SERMOLLI, 1951: 34) should be reconsidered. Secondly, staminodes were normally observed around drupes (see below), thus revealing that the pistillate flower of the section is potentially bisexual in also having the other sex in unfunctional condition, as is its staminate flower (see above); in addition, these staminodes had four pollensacs like stamens (see below). Neither of these characters was observed in any other section of *Pandanus*.

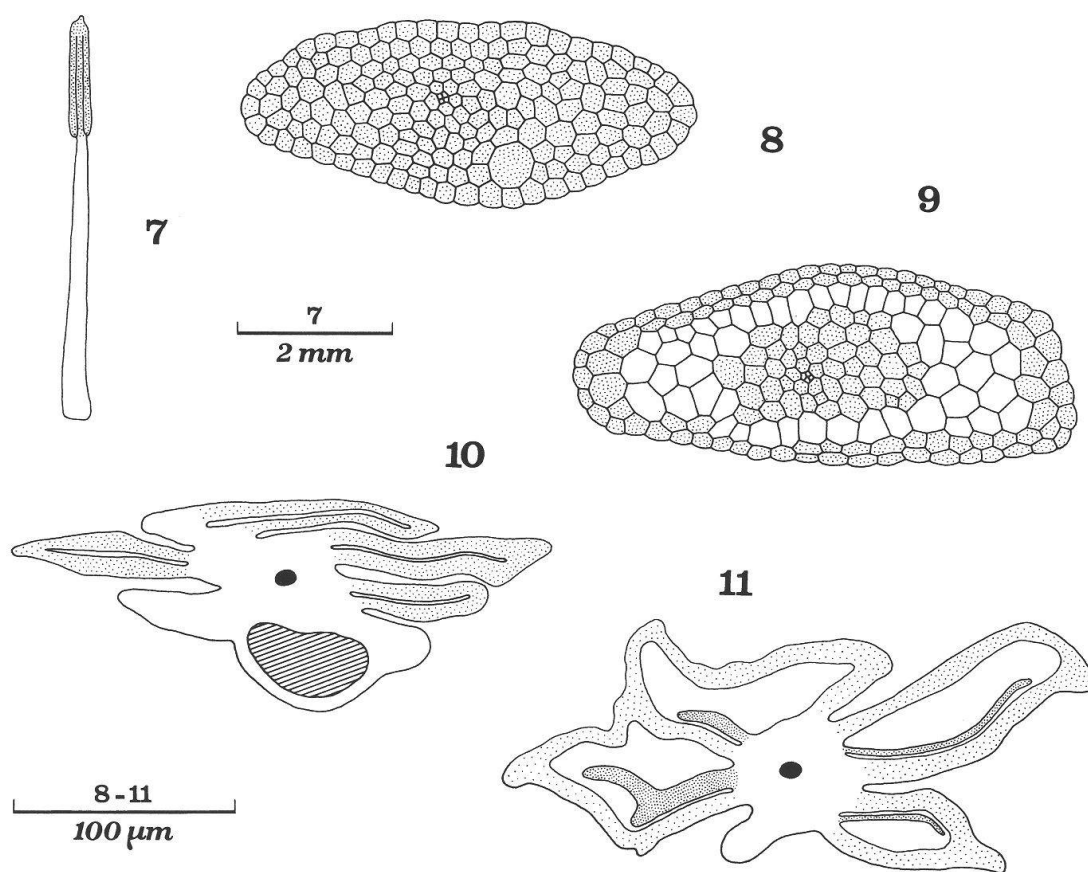
With such a large number of exclusive characteristics, sect. *Martellidendron* can be easily recognized, either with pistillate or staminate plant. Therefore a glance at the stigmas of *P. nosibicus* (fig. 3) readily revealed that it is a member of this section.

The point here is to ascertain the identity of this species within sect. *Martellidendron*. To date, four species only were known in the section: *P. androcephalanthos* Martelli (both pistillate and staminate plants known), *P. cruciatus* Pic. Serm. (only pistillate plant known), *P. hermaphroditus* Martelli and *P. kariangensis* Huynh (only staminate plants known). A preliminary investigation of the leaf micro-morphology of *P. nosibicus*, using the method described in HUYNH (1971) for observing the leaf surface, readily revealed that it is distinct from these four species. Indeed, the abaxial face of its leaf is entirely smooth; that is to say: no processes of any sort exist either on the stomates or the non-stomatic epidermal cells. This absence of processes was quite unexpected since the face has processes in the other four species. Actually, in *P. kariangensis* it is abundantly verrucate: both the polar cells in stomates and the non-stomatic epidermal cells around stomates have several verrucas (HUYNH, 1981: fig. 36). In *P.*

androcephalanthos, *P. cruciatus* and *P. hermaphroditus*, the polar cells have verrucas or a branched papilla, and so do several non-stomatic epidermal cells (HUYNH, 1979: 368). From another point of view, the absence of any processes on the abaxial face of the leaf of *P. nosibicus* would suggest that this species is isolated within sect. *Martellidendron*. This is further supported by the fact that this species has a flat pileus (fig. 4), a feature to date unique in the section.

In gross morphology also, *P. nosibicus* can be distinguished from the other four

species. From *P. androcephalanthos* and *P. cruciatus*, it differs in its syncarp, pileus, and endocarp. Its syncarp is oblong cylindric (fig. 12) and about 25 cm long; its drupe has a flat pileus (fig. 4); its endocarp a \pm flat top (fig. 5). In *P. androcephalanthos*, the syncarp is oblong conoid, its total length not known; the drupe has a dome-like pileus; the endocarp an acute top (MARTELLI & PICH-SERMOLLI, 1951: fig. 3f). This wide difference between *P. nosibicus* and *P. androcephalanthos* is most remarkable since these are closely sympatric, the latter species being also found in



Figures 7-11: *Pandanus nosibicus* (holotype) (7-10) & *P. sp.* (*Callmender & Laivao NEU 8*) (11). 7: Staminode, showing anther (dotted) and filament. 8, 9: Middle and upper transverse section of staminode filament respectively (dotted: lignified cells; vascular bundle represented by smallest cells). 10, 11: Middle transverse section of staminode anther (sparsely dotted: pollensacs; densely dotted: pollensac partitions; hatched: raphide cell; black: vascular bundle). **Note:** Staminodes were rehydrated in 65°C water, embedded in paraffin, microtome-sectioned, stained in Safranin-Astrablue, and mounted in Eukitt, a synthetic resin.

Lokobe (MARTELLI & PICH-SERMOLLI, 1951). In *P. cruciatus*, the syncarp is oblong conoid and 45-50 cm long; the drupe has a pyramidal acuminoid pileus; the endocarp is prolonged upwards with two cusps (MARTELLI & PICH-SERMOLLI, 1951: fig. 1g).

With regard to *P. kariangensis*, *P. nosibicus* differs in its leaf. This is stiff coriaceous and 6 cm wide in middle; the abaxial face untessellate; the prickles dark brown at tip, brownish below like the blade; the apical angle of the blade (flattened horizontally) beneath the cauda very narrow, about 6° (fig. 1). In *P. kariangensis*: the leaf is flexuous subcoriaceous and 3.8 cm wide in middle; the abaxial face tessellate almost throughout; the prickles entirely dark brown; the apical angle of the leaf blade about 14° (HUYNH, 1981).

With regard to *P. hermaphroditus*, *P. nosibicus* also differs in its leaf. The leaf of *P. hermaphroditus* has not been described. This knowledge gap was a drawback for the identification of unknown

species in sect. *Martellidendron* in the past. Fortunately, the present author was recently able to observe the leaf, using one of the four sheets composing the type of *P. hermaphroditus* (Perrier 11010) in Paris. The sheet comprises only upper parts of leaves and bracts, as indicated by a label found on it («extrémités de bractées et de feuilles»). The longest is about 70 cm long. They are so similar that it was not possible to determine which were from leaves and which from bracts. All are greenish at both faces the abaxial face lighter, strongly revolute, and terminated by a dark brown tip contrasting with the greenish lower parts; the longitudinal veins slightly distinct at the adaxial face, more so at the abaxial face; no transverse veins visible (hence the blade untessellate) at either face; the prickles on both margins and midnerve brownish along their lower part but brown to slightly dark brown at tip; the midnerve armed throughout; the pleats indistinct and not canaliculate; the uppermost part very narrow along a long course and therefore resembling a flagellum. As

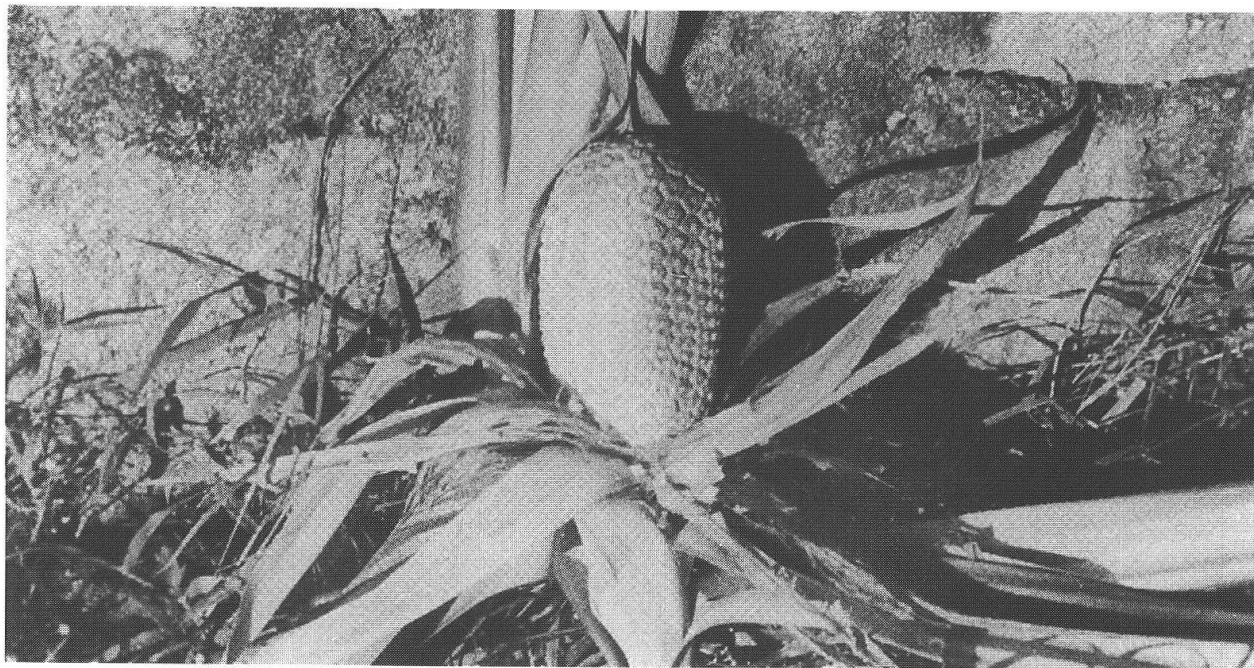


Figure 12: *Pandanus nosibicus*. Syncarp (photo Laivao).

described, the leaf of *P. hermaphroditus* is quite different from that of *P. nosibicus*. In particular, it is so gradually attenuate that the apical angle of its blade hardly makes 1-2° (fig. 6). In order to know how these two species differ from one another in this respect, compare the longest leaf piece of *P. hermaphroditus* (fig. 6) with the upper part of the leaf of *P. nosibicus* (fig. 1). The leaf piece is about 2.4 cm wide at 70 cm from the apex, 0.8 cm at 35 cm, thus narrowing quite differently from the upper part of the leaf of *P. nosibicus* which is about 4.5 cm wide at the former level and 3.5 cm at the latter level.

Further notes on the staminodes of Pandanus nosibicus

As mentioned above, the drupes preserved on the type of this species were separated when collected. Despite the separation which must have removed staminodes, most drupes still showed staminodes (fig. 4) when studied. Each staminode found was located in a longitudinal groove at the drupe base, more precisely at the lowermost level of the nitid epicarp. Longitudinal grooves being observed all around every drupe, it seems therefore that the drupe of *P. nosibicus* has staminodes around its base. These grooves are remote by 0.7-1 mm; as a consequence, staminodes seem similarly remote on the drupe base; this remoteness however should be further verified using entire syncarps.

These staminodes are 1.6-4.2 mm long and comprise a filament and an anther (fig. 7). Both vary in length, width, and ratio between them. A vascular bundle is observed in each staminode, and it terminates a little below the staminode apex. The filament is oblong elliptic in transverse section, and is entirely lignified (fig. 8) except for the uppermost part where it is only partially so (fig. 9). The anther is oblong and acuminate (fig. 7), and has four pollensacs and one or two large raphide

cells (fig. 10). At this stage of development (viz. full maturity of fruits), the pollensacs are strongly compressed; therefore it was not possible to observe the structure of their walls except for the epidermis which is still distinct; nevertheless, it was ascertained that they have neither pollen nor endothelial thickenings. These pollensacs are separate from each other (fig. 10), by contrast with the pollensacs in a stamen anther. This unusual feature should be further verified, using fresh staminodes at a younger stage.

From another point of view, the fact that the staminode anther of *P. nosibicus* is acuminate (fig. 7) seems to indicate that its stamen anther is acuminate as well, and, consequently, that this species belongs to subsect. *Martellidendron* (where stamen anthers are acuminate: HUYNH, 1981), and not to subsect. *Retusiflora* (where stamen anthers are retuse: HUYNH, 1981). Actually, in *Freycinetia*, another genus of the family Pandanaceae, staminodes were also observed in the pistillate flowers, and their anthers were similar to the stamen anthers in being retuse (HUYNH, 1992).

The normal presence of staminodes around drupes and of four pollensacs in these staminodes, as observed in *P. nosibicus*, seems to be common to the members of sect. *Martellidendron*. Actually, in the unknown species mentioned above (*Callmander* & *Laivao* NEU 8) and in which the present author was able to use a whole syncarp, each drupe observed also showed staminodes around its base and these also had four pollensacs (fig. 11). Consequently, it would be of interest to further tentatively observe these two features in the syncarps of *P. androcephalanthos*, *P. cruciatus*, *P. hermaphroditus* and *P. kariangensis*, in all of which no existence of staminodes was recorded.

Also, the staminodes of that unknown species showed a feature not observed in the stamens of angiosperms. That is: in the staminodes whose anther was not com-

pressed, a partition was found within each pollensac, and consequently, each staminode had four partitions (fig. 11). Most probably partitions also exist within the staminode pollensacs of *P. nosibicus* but these were so strongly compressed (fig. 10) that it was not possible to observe if they had partitions or not. By contrast, the stamens of angiosperms have only two partitions, each in the middle of an anther lobe (see for example HUYNH, 1991: fig. 5). However, this unusual feature was not suitably observed given the advanced stage of development of the syncarp: indeed, except for the partitions, the other cells within the pollensacs have disappeared (fig. 11). Therefore, it should be studied further, using fresh staminodes at a younger stage.

Sect. *Martellidendron* is the first section known in the genus *Pandanus* to have pistillate flowers normally with staminodes, and staminodes with four pollensacs like stamens; most probably it is the only section. In addition, as mentioned above, its staminate flowers invariably bear a pistillode. Thus, both the pistillate and staminate flowers of the section are potentially

bisexual by also having the other sex in unfunctional condition. This potential bisexuality recalls the genus *Freycinetia*, where potential bisexuality was also observed in both flowers and staminodes also have four pollensacs (HUYNH, 1991, 1992). This close relationship would be correlated to another, which is that both *Freycinetia* and sect. *Martellidendron* have a 3-layered exine, a structure not observed in any other section of *Pandanus* (HOTTON *et al.*, 1994). For these reasons, sect. *Martellidendron* appears to constitute the phylogenetic link between these two genera. This will be tentatively tested in a near future at the Laboratoire de Phanérogamie, University of Neuchâtel, using molecular data.

ACKNOWLEDGEMENTS

The author is deeply indebted to the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, and the Missouri Botanical Garden, St. Louis, for the loan of materials. He is desirous of extending his gratitude to Michel Omer Laivao for additional field notes on *P. nosibicus*.

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